FALSE-PARASITIZED COCOONS AND THE BIOLOGY OF AIDIDAE (LEPIDOPTERA: ZYGAENOIDEA)

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Abstract.—Two or four holes in the outer mesh of cocoons in Aididae appear to mimic exit holes of parasitic Hymenoptera. Cocoon construction in *Aidos amanda* (Stoll) from Venezuela is described and documented with photographs, along with notes on its biology. *Annona punicifolia* is reported as a larval hostplant of *A. amanda*. Literature on the cocoons and biology of Aididae are reviewed. Citations of Guyaba as a larval hostplant of *A. amanda* are considered to be erroneous based on misidentified larvae. Scenarios for the evolution of cocoon construction in Aididae are discussed, as are possible functions of the false exit holes in their cocoons.

Key Words: Lepidoptera, Aididae, cocoon construction, predator avoidance, false-parasitized cocoons

The small Neotropical family Aididae (6 species), previously placed as a subfamily of Megalopygidae, is an important link in the understanding of the relationships among Limacodidae, Megalopygidae and Dalceridae (Epstein in press). Larval aidids differ from many larval megalopygids in lacking plumose setae on the dorsum, and in absences of verrucae below the spiracles and of large membranous pads on the abdominal prolegs (Epstein in press). Their two rows of urticating bristles on the dorsum of the abdomen are sunken in repose and splayed out in rosettes when stimulated (Hopp 1935; Epstein in press).

The earliest known description of aidid cocoons was given in a letter by Moritz (published in Klug 1836). They were described and figured by Dewitz (1878: 20–26; pl. 1, figures 17–18), based on notes and specimens from Gollmer. Hopp's (1930, 1935) descriptions were based on those of the earlier workers, though they were not cited in his later publication (Hopp

1935). Cocoons of *Aidos amanda* (Stoll) were described as "... spun on the underside of leaves of different trees, look like the webs of ichneumon-flies [perhaps meaning a parasitized wasp cocoon], especially since also their hiding places [emergence holes of braconids–from earlier literature; see discussion] are copied" (Hopp 1935:1072; english version). Forbes (1942:396) described the cocoon as "... with trap door, silken stem for suspension and one or two pairs of rounded depressions in the sides (varying in individuals of a single batch of *A. amanda*)."

Descriptions of the cocoon and other immature stages of *A. amanda* by Hoffmann (1932) were based on misidentified Megalopyginae. This is deduced from features of the larvae described by Hoffmann, which occur in megalopygids and not in aidids. These include (1) matted wool covering the eggs (from the caudal end of the female abdomen); (2) plumose setae, and a fleshy knob behind every spiracle in the larva; and (3) larval setae woven into the cocoon. Along with photographic documentation, I will describe the cocoon construction of a species believed to be *A. amanda*. I also report its life history, update the hostplant literature on aidids, discuss alternative functions of the false exit holed cocoons, and present evolutionary scenarios that may have brought them about.

METHODS

I reared a single aidid larva from Venezuela (see locality data below). It was recognized as an aidid from the description in Hopp (1935) and from specimens examined at the Natural History Museum, London (BMNH). Although the larva perished in its cocoon as a prepupa, I tentatively identified the species as A. amanda based on adult males and females collected from the same locality in September 1990, a location where only one species of Aidos is known to occur. These specimens closely match the types of A. amanda figured in Stoll (1782, pl. 383, figs. C, D). The genitalia of the Venezuelan and other aidid species examined appear to be rather uniform. However, further evidence in support of the identity of this population as A. amanda is found in the labial palpus, which has only two segments; three are found in other aidid species and in museum specimens labelled as A. amanda from outside of Venezuela and the Guianas. The two-segmented palpus matches those of a specimen believed to be A. amanda from Guyana (Cornell University Coll.), the closest locality of any specimen examined to its Surinam type locality. Voucher specimens of adults, the larva and its skins are deposited in the entomological collection of the National Museum of National History, Washington, D.C. (USNM). Although the cocoon was lost, another cocoon from the same locality in Venezuela is placed in the USNM collection. Additional aidid specimens examined and the institutions where they are deposited, include: adults (USNM, BMNH, and Universidad Central de Venezuela, Maracay); larvae (BMNH);

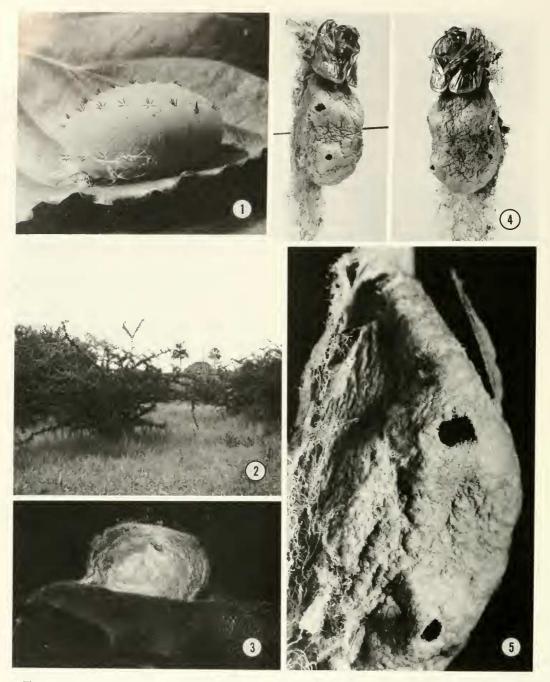
and cocoons (USNM, BMNH and Cornell University).

LIFE HISTORY

The presumed larva of A. amanda was found in the Venezuelan llanos at Hato Masaguaral, Edo. Guarico, 45 km S. Calabozo (8.57°N, 67.58°W), 75 m elevation on 9 July 1989 (Fig. 1). The larva was feeding on a leaf of Annona punicifolia Triana and Planch at ca. 1400 h in cloudy conditions during a light rain. The larva was attached to the underside of the leaf. with its prothorax visible from above at the consumed leaf apex. The Annona bush was on the edge of a savanna that is often inundated during the rainy season (Fig. 2). In a plastic rearing container, the larva spun silk trails when moving between leaves and a silk pad on the leaf it was feeding on. When pulled from a leaf the larva would often remain motionless in the bottom of the container, with silk hooked to its crochets. Locomotion is described in Epstein (in press).

The larva had seven or eight instars, based on the assumption that it was a second or third instar when first discovered (Table 1). Stadia lasted from at least six to thirteen days, though the larva was reared under a wide range of climatic conditions. It was fed the native hostplant *A. punicifolia* until the fifth or sixth instar when it was switched to oak (*Quercus* spp.). It preferred oak when later given a choice of leaves of an annonaceaeous tree during its final stage.

Cocoon construction.—On 9 September the prepupa began spinning the cocoon between two leaves (Fig. 6) in figure-eight fashion. The final frass pellet was light brown and the prepupa became wetted down, similar to what occurs with Limacodidae (McNaulty, 1967; Epstein in press). By 10 September the prepupa had spun a thin outer mesh with one small oval hole on each side (approx. 1 mm). Each hole had a more dense reinforcement of silk around its edges, roughly a third the distance from



Figs. 1–5. 1, late instar larva of *Aidos amanda* (photo by K. V. Sandved); 2, habitat and *Annona punicifolia*, hostplant of *A. amanda*, at Hato Masaguaral, Venezuela; 3, recently completed cocoon of *A. amanda* (hatch end); 4, laterodorsal view of four-holed aidid cocoon with emerged pupal exuvia (photo by V. Krantz); 5, detail of aidid cocoon, hatch above (hole above 3 mm across) (photo by L. Minor-Penland).

Table 1. Life history of *Aidos amanda* (Stoll). Dates of molting, approximate instar and host for one individual reared to prepupa.

Date	Specimen	Instar/ Cocoon	Host
09 vii		2–3	Annona
15 vii	_	3-4	Annona
22 vii	skin	4–5	Annona
04 viii	skin	5-6	Annona/Quercus
12 viii	skin	6-7	Quercus
25 viii	prepupa	7-8	Quercus
9–12 ix		cocoon	

one end of the cocoon (Fig. 7). From inside the cocoon the emerald green prepupa made the holes very apparent. On 11 September the larva constructed a u-shaped escape hatch on the end of the cocoon near the holes, reinforcing the edge of the hatch with silk in much the same manner as the holes. The "holes" were sealed on the inside of the cocoon by 700 hrs on 12 September.

Other hostplant records for Aididae .---Gollmer reported A. amanda on sweet orange (from Dewitz 1878). Since Hoffmann (1932) misidentified a megalopygid as A. amanda, it follows that his hostplant record for Aidos on Guyaba (probably Inga sp.) is also incorrect. Hoffmann's hostplant record was later cited in Hopp (1935:1072, 1098) and Lima (1945). An adult specimen of Aidos yamouna (Dognin) from Peru in the USNM collection was reared on Cinchona ledgeriana, Moens. 1876 (Rubiaciae). This is a quinine-yielding tree, with leaves "perfectly glabrous on both surfaces," originally from Rio Mamore, Bolivia (Trimen 1881).

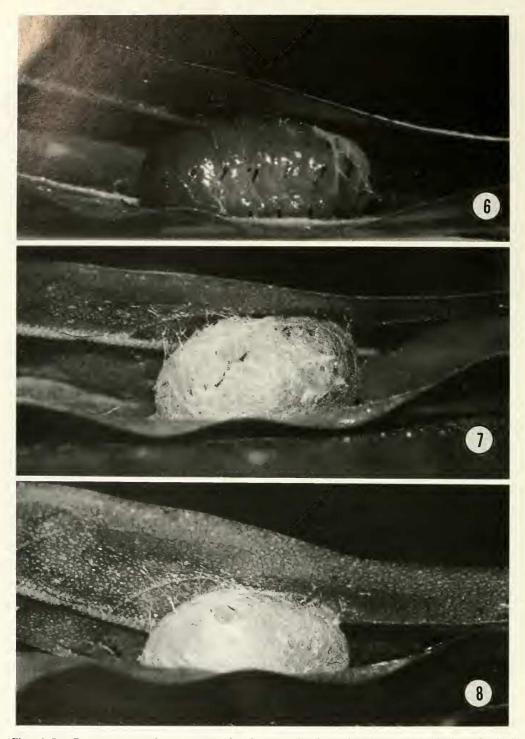
DISCUSSION

The close resemblance of their false exit holes to emergence holes of parasitic Hymenoptera may protect aidid cocoons from vertebrate predators. If vertebrates indeed learn that parasitized cocoons have little or no food to offer, as suggested by Hinton (1955), then it is also reasonable to hypothesize that they would tend to avoid cocoons constructed with false holes. This view was expressed by Dewitz (1878) as it related to the cocoons of *A. amanda*.

Hinton's (1955) review of protective devices in Endopterygote pupae did not include A. amanda, from the literature mentioned above, or other examples of "false exit holes" in Lepidoptera cocoons. His one example of a chrysalis considered it to mimic parasitized galls (Agriolaus maesa, Lycaenidae) (from Eltringham 1923:89-90). Hinton's other examples of possible predator-avoidance mechanisms included moth cocoons that appear to have parasitoid wasp cocoons extruding from them (e.g. Deilemera antinorii Oberthur; see Eltringham 1923:83, figure 32). Similarly, some species of ichneumonids build a false cocoon outside of the skin of their larval host, complete with a false emergence hole, while their true cocoon is inside the dead host (e.g. Hyposoter parorgyiae and H. rubiginosa; Finlayson 1966 and R. Carlson pers. comm.).

The characterization of aidid cocoons as having the appearance of "webs of ichneumon-files" in the earlier literature is confusing (e.g. Hopp 1935), since ichneumonids do not build webs other than cocoons. The "webs" may refer to large ichneumonid cocoons, or groups of smaller braconid cocoons with emergence holes in them, as suggested in Klug (1836). Dewitz (1878: 24) thought they resembled a parasitized cocoon of a tenthredinid.

The evolutionary development of false exit holes in aidids may have been an offshoot of hatch construction. This is plausible because two holes in all examples are in close proximity to the hatch, and the prepupa appears to reinforce both holes and hatch in similar fashion. The cladogram of the limacodid group (Epstein in press) indicates that hatch construction in Aididae is plesiomorphic, and that false exit holes are uniquely derived (autapomorphic). Another autapomorphic feature in aidids, the flexible and amorphous apex of the spinneret (Figs. 10–12), may be useful in shaping and reinforcing the silk around the holes.



Figs. 6–8. Cocoon construction sequence of *Aidos amanda:* 6, wetting down and beginning of spinning between two leaves; 7, at first visible sign of holes (note spines visible through hole); 8, outer mesh near completion, prior to filling in of holes.



Fig. 9. Nest of *Polybia occidentalis bohemani* in Costa Rica.

The false exit holes may be functionally related to hatch construction in the following way. They allow the prepupa to view the immediate environment to select optimal hatch placement for future adult emergence. This "window" hypothesis is supported by my observations that the prepupa constructs the holes prior to the hatch. Moreover, in cocoons examined with a single pair of holes, the hatch is constructed at the same end of the cocoon. This suggests that with proper stimuli, no further holes are made. Even if the holes were to function in selecting hatch placement, this would not preclude them from having a predatoravoidance function as well.

Forbes's (1942) observations, quoted above, suggest a flexibility in the number of holes constructed within *A. amanda*. However, the hole arrangement of a fourholed cocoon (USNM, no data or adult voucher) suggests that the number of holes may be fixed in an individual. In this cocoon one of two hole sites proximate to the



Figs. 10–12. Spinneret of larval Aididae (exuviae from two specimens) (scale length in parentheses): 10–11, Aidid sp. from Brazil (BMNH); 10, ventral view of spinneret, flexible apex is folded down (arrow), silk pore with silk is above (46 μ m); 11, dorsolateral view (100 μ m); 12, Aidid sp. from Brazil (BMNH), dorsal view of spinneret, apex is extended (20 μ m).

butch was apparently blocked by a stem at the time of construction. The prepupa constructed a smaller hole between the two holes posterior to the hatch, perhaps to compensate for the missing hole in the usual location.

False holes may also give aidid cocoons the appearance of being small nests of vespids, or of other nest-building wasps, that are built on the undersides of leaves (e.g., *Polybia occidentalis bohemani*; Fig. 9). The "holes" on the cocoons could appear as nest entrances, though smaller in size (1 to 3 mm compared to approx. 9 mm for nest entrance in Fig. 9).

Experimental studies are needed to determine whether there is less predation on aidid cocoons compared to similar cocoons without false exit holes (e.g., in megalopygids). Other future research should be undertaken to determine whether the number of holes are fixed or flexible in a given species or between species of Aididae.

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